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THE AUDITORY REGION OF AN UPPER
PLIOCENE TYPOTHERID

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RESULTS OF THE FIRST MARSHALL FIELD PALEONTOLOGICAL EXPEDITION
TO ARGENTINA AND BOLIVIA, 1922-24

A thorough account of the otic region of *Typotherium cristatum* (Serres) has been given by Van Kampen in his classic work "Die Tympanelgegend des Säugetier-schädels" (1905, pp. 610-613). A few new features are brought out in the present study and certain of Van Kampen's homologies are re-interpreted. The auditory region of *Pseudotypotherium*, as here understood, agrees in essentials with that of other notoungulates previously described by me (1932). The description given below has been taken from American Museum No. 14509 and has been written to serve as a basis of comparison in connection with the study of the Typotheria from the Deseado and Colhué-Huapí beds of Patagonia collected by the First Marshall Field Expedition of Field Museum (1922-24) and by the Scarritt Patagonian Expedition of the American Museum (1930-31).

I wish to express my thanks to the authorities of the American Museum for their kindness in permitting study of this and other specimens, and to Mr. Carl F. Gronemann, Staff Illustrator, Field Museum, for his painstaking work on the figures.

***Pseudotypotherium pseudopachygnathum*¹ (Ameghino).**

Horizon.—Monte Hermoso beds, upper Pliocene.

The *auditory bulla* in the Typotheria has hitherto been regarded as simple and hollow; Van Kampen, in describing the bulla of *T. cristatum*, states that it is *wahrscheinlich hohl*. Recently conducted investigations on the internal structure of typotherian bullae,

¹ For synonymy see Kraglievich (1934, pp. 35-36, and references). *Pseudotypotherium* is very close to *Typotherium*, the principal distinction being that in the Monte Hermoso genus the palatal constriction at the anterior end of the maxillaries is very slight, whereas in the Pampean genus it is pronounced.

which will shortly be published, show that a septum bullae is present in the genera investigated. The bullae of the specimen under discussion have not been opened, but, to judge from the conditions observed in the closely related Pliocene genus *Typotheriopsis*, are probably compound and composed of an entotympanic in addition to the tympanic. In *Typotheriopsis* the sinus hypotympanicus is finely cancellous while the cavum tympani is hollow; in the American Museum specimen of *P. pseudopachygnathum* cancellae are visible in the broken anterior portion of the right bulla. The ventral wall of the bulla in *T. cristatum*, as figured by Roth (1903, Plate 3, Fig. 4), is very dense and thick. I have observed the same condition in *Typotheriopsis*.

Van Kampen's description of the external appearance of the bulla of *T. cristatum* applies almost equally well to the specimen under consideration. Some minor differences may, however, be

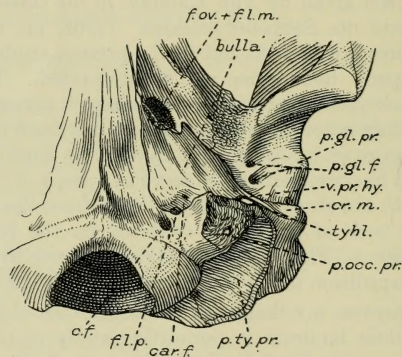


FIG. 7. *Pseudotypotherium pseudopachygnathum* (Ameghino). Basicranial region of left side, ventral view. A.M. No. 14509. x 2/3. c.f., condylar foramen; car.f., carotid foramen; cr.m., crista meati; f.l.p., foramen lacerum posterius; f.ov. + f.l.m., foramen ovale and foramen lacerum medium; p.gl.f., post-glenoid foramen; p.gl.pr., post-glenoid process; p.occ.pr., paroccipital process; p.ty.pr., post-tympanic process; tyhl., tympanohyal; v.pr.hy., vagina processus hyoidei.

noted. The ventral margin of the bulla bears a slight keel, more prominent on the right than on the left, which merges anteriorly with the styliiform process. There appears to be no distinct process from the ventral margin abutting against the paroccipital process in this species, the junction between tympanic and paroccipital process being practically a straight, transverse line. The two bones are in simple contact and do not present an interlocking sutural union as they do in certain interatherids. The spine, by which the

bullae comes in contact with the basisphenoid, is somewhat longer and narrower in *P. pseudopachygnathum* than in *T. cristatum*. It extends anteriorly as a thin wedge between the basisphenoid and the alisphenoid.

There is no definite line of demarcation on the ventral surface of the bulla which would indicate the limits of the entotympanic and the tympanic. From a comparison with *Typotheriopsis*, however, it may be stated with some confidence that the anterior and mesial thirds of the bulla are formed by the entotympanic.

The *tubular meatus* is large, and runs postero-externally in a slightly upward direction. The porus acusticus externus is circular and bounded dorsally and posteriorly by the squamosal, anteriorly and ventrally by the tympanic. The ventral border is formed by a lip projecting posteriorly from the crista meati,¹ a feature characteristic of the Toxodonta and Entelonychia but lacking in the Intertheriidae and Hegetotheriidae, due to the absence of a well-defined crista meati in members of these families. The portion of the tympanic forming the anterior boundary of the porus is firmly fused with the post-glenoid process, as was noted by Van Kampen in *T. cristatum*. This author goes on to state that there are two ridges on the under wall of the meatus in this form, of which the anterior passes into the glenoid fossa. The posterior ridge, according to his description, lies behind the stylomastoid foramen (see below) and lateral to the paroccipital process; it extends upwards behind the porus, forming the external portion of the occiput. He considers this posterior ridge to be the homologue of the post-tympanic process (pars serialis) of the squamosal in *Toxodon*, an identification which is unquestionably correct. Exception must be taken, however, to the statement that this post-tympanic process is a ridge from the ventral wall of the meatus.² The process is in contact ventrally with the tympanic in the vicinity of the vagina processus hyoidei but passes upwards behind the meatus in *P. pseudopachygnathum*, and indeed in every notoungulate examined by me. It seems unlikely that *T. cristatum* would be distinct from the rest of the order in this respect.

¹ An abbreviation for the cumbersome term "crest on the under surface of the tubular meatus." I previously (1932, p. 8) employed "tympanic crest" as an alternative, but this term is liable to be misleading as its Latin equivalent, crista tympanica, is applied to the margin of the sulcus tympanicus. Roth (1903, p. 19) applied the name processus tympanicus to this crest. This, however, is too ambiguous as there are several closely comparable terms in existence, such as processus tympanicus petrosi, alisphenoides, etc., which might lead to confusion.

² Roth (1903, p. 19) also held this opinion.

The structure called the anterior ridge by Van Kampen is unquestionably the crista meati. As in *T. cristatum* it is indistinguishably fused with the post-glenoid process of the squamosal, the fissura glaseri being confined to the anterior half of the squamoso-tympanic contact. As a result of this fusion Van Kampen was in some doubt

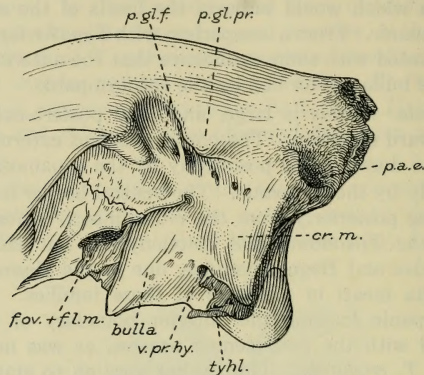


FIG. 8. *Pseudotypotherium pseudopachygnathum* (Ameghino). Cranial region of left side. Lateral and a little obliquely ventral view. A.M. No. 14509. $\times 2/3$. *cr.m.*, crista meati; *fov. + f.l.m.*, foramen ovale and foramen lacerum medium; *p.a.e.*, porus acusticus externus; *p.gl.f.*, post-glenoid foramen; *p.gl.pr.*, post-glenoid process; *tyhl.*, tympanohyal; *v.pr.hy.*, vagina processus hyoidei.

as to whether this crest was from the meatus or whether it was a continuation of the post-glenoid process. From comparisons with other notoungulates it is at once apparent that it is from the meatus. The crista meati in *P. pseudopachygnathum* bears a prominent, ventrally directed process or spine on its infero-external angle, precisely as in toxodonts (*sensu strictu*). Van Kampen describes two of these spines on the crest of *T. cristatum*. This author considered that *Typotherium* might have possessed a meatus spurius, but this is certainly not the case.

The *vagina processus hyoidei* is rather large and deep, and is situated at the posterior end of the bulla halfway down its lateral side. Mesially, anteriorly and laterally it is bounded by the tympanic, posteriorly the post-tympanic process of the squamosal appears to form part of the wall. As in most typotheres, the paroccipital process does not enter into the boundary of the vagina; this is not a condition prevailing throughout the suborder, however, for in some genera, e.g. *Cochilius*, the paroccipital process forms a part of the posterior wall. A portion of the tympanohyal is still

in place in the vagina of the left side. Van Kampen states that the stylomastoid foramen in *T. cristatum* lies between the tympanic and the post-tympanic process. This is correct but his figure would indicate that what he identified as the foramen is really the vagina processus hyoidei.

The *epitympanic sinus* is very large and hollow; it is noticeable externally on the occipital surface. Roth (1903, Plate 3, Fig. 4) gives an excellent cross-section figure of the sinus in *T. cristatum*.

The *mastoid process* is visible on the occiput as a thin strip of bone dorsal to the exoccipital. It merges laterally with the post-tympanic process of the squamosal. This latter feature suggests the possibility that the "adventitious bone" previously described by me (1932, p. 19) may represent an enlarged, plate-like mastoid process. This does not seem probable, however, in view of the fact that the mastoid process in the Toxodonta and Typotheria is known to be of small size. Furthermore, if this supposed neomorph (which only occasionally appears) was in reality the mastoid process one would expect to find the suture between it and the post-tympanic

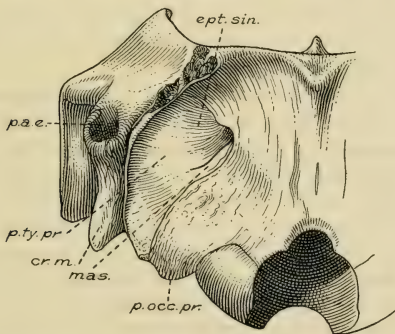


FIG. 9. *Pseudotypotherium pseudopachygnathum* (Ameghino). Occipital region of left side. A.M. No. 14509. x 2/3. *cr.m.*, crista meati; *ept.sin.*, epitympanic sinus; *mas.*, mastoid; *p.a.e.*, porus acusticus externus; *p.occ.pr.*, paroccipital process; *p.ty.pr.*, post-tympanic process.

process in the majority of young skulls. Actually the reverse is the case (see, in this connection, Van Kampen's figure of the occiput of a young *Toxodon platensis*, 1905, p. 618, fig. 79).

Elements touching the external surface of the bulla.—Anteriorly the bulla sends forward a spine (see above) which extends between the ali- and basisphenoid; laterally it is in contact with the alisphe-

noid and squamosal, mesially with the basioccipital, and posteriorly with the paroccipital process and the post-tympanic process. The tympanohyal lies mainly in the lateral wall of the bulla.

The adjacent foramina.—Eustachian canal not visible; Van Kampen reports the same condition in *T. cristatum*. Possibly confluent with the ovale and lacerum medium.

Foramen ovale and foramen lacerum medium:¹ confluent, forming a large oval opening in the alisphenoid.

Foramen lacerum posterius: situated at the postero-internal corner of the bulla on the suture between the bulla and the exoccipital.

Carotid foramen: small, orifice situated in the posterior wall of the bulla antero-external to the orifice of the foramen lacerum posterius.

Condylar foramen: large, immediately postero-internal to the foramen lacerum posterius.

Stylomastoid foramen: opens externally in the cleft between the crista meati and the post-tympanic process; orifice somewhat closer to the vagina processus hyoidei than to the porus.

Post-glenoid foramen: situated a short distance behind the glenoid articulation; orifice divided into two parts by a small bridge of bone lying transversely across it.

A variable number of small vascular foramina extend posteriorly from the post-glenoid foramen to the squamoso-tympanic junction.

The arrangement of these foramina conforms, in the main, to the usual notoungulate pattern. Two exceptions may, however, be noted. The post-glenoid foramen is placed considerably farther forward than is usual in the order, a condition which is perhaps due to the fusion of the post-glenoid process with the squamosal. The position of the carotid foramen differs somewhat from that seen in other families of the suborder. In the Hegetotheriidae this foramen is situated between the basioccipital and the mesial side of the bulla, while in the Interatheriidae it lies behind the bulla and immediately mesial to the foramen lacerum posterius (Sinclair, 1909). A comparison with *Typotheriopsis* indicates that *Pseudotypotherium* agrees more closely with the Interatheriidae than with the Hegetotheriidae in this respect. In *Typotheriopsis* the foramen lacerum posterius and the carotid foramen are in the same position as in the

¹ I previously stated (1932, p. 23) that these foramina were apparently separated by a septum in a skull of *Cochilius volvens*, F. M. No. P13424. Examination of an excellently preserved skull of the same species collected by the Scarritt Patagonian Expedition (A. M. No. 29651) shows that this is not the case.

interatherids but have an antero-posterior, rather than a transverse, alignment.

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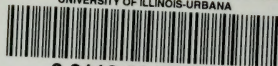
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